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Morphological mimicking and defense mechanism between the hosts and mistletoe: *Dendrophthoe falcata* of Loranthaceae

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ABSTRACT

Dendrophthoë falcata (L.f.) Ettingsh., is a non-host specific mistletoe, commonly found along the Coromandel Coast of Tamil Nadu. The literature screening was found the host range, haustorium formation and types, molecular and genetic evolution of the family, but the morphological, anatomical and phyto-chemical relationships between them are not known. The current study attempted to test the Batesian mimicry concept and based on the haustorial morphotypes three types of defense mechanism was established. For which bark, lenticels, branchlets cut end, epicortical root, leaf area, and leaf thickness of host and parasite was studied and compared. Botanical inventory was conducted, sampled and photographed from four vegetation areas for a period of six months. The analysis showed positive relationship between the leaves (75%) and stem (65-70%) attributes of host and parasitic. Three kinds of defense mechanism were synthesized and described them in detail with pictures from three different haustorial morphotypes.

Keywords: *Dendrophthoë*, Defense mechanism, Haustorium, Morphotypes, India

1. INTRODUCTION

The Indian subcontinent mistletoe, *Dendrophthoë falcata* (L.f.) Ettingsh. of Loranthaceae is grows on a great number of native as well as introduced trees, shrubs and climbers in different habitats including saline environments (Arumugam *et al*., 2015). However, the range of distribution on a landscape scale and host-parasite interactive responses between the two was not well understood yet, but it mostly predicted that the mistletoe infection was positively related to tree size, water, nutrient status and canopy cover (Press and Phonenix, 2005). The study on host range have been studied since long by different authors in India (Fischer, 1926; Ezekiel, 1935; Sayeeduddin and Salam, 1935; Lacy, 1936; Sayeeduddin and Waheed, 1936; Mathur, 1949; Singh,

1959; Murthy, 1960; Sampathkumar and Kunchithapatham, 1968; Ghosh, 1970; Das and Ghosh, 1999; Selvi and Kadamban, 2009; Thriveni *et al*., 2010; Vijayan *et al*., 2015; Rothe and Maheswari, 2017). Besides it is necessary and challenge to understand how the angiospermic parasites are interacts with their host from species to species in an environment (Arumugam *et al*., 2015).

This parasite affects the host's vascular resources to extract water, nutrients, and organic compounds which lead to the host productivity (Scholes *et al*., 1999) and the extent to which this impact on host performance was depends upon the degree of autotrophy of the parasite. The influence of mistletoes on their hosts might be reduced growth rates and vigour, sparse foliage, malformation of woody tissues, poor fruit yield or seed set, top dying, disease attack and premature death (Arumugam *et al*., 2015). Meanwhile Rispail *et al*., (2007) studied relative ability between the host and parasite and their tolerance or resistance to attract resources from the host species. The present work was framed to study the similarity in morphological features between them and to know how they are interact and defence each other to derive or regulate the water and nutritional resources.

2. MATERIALS AND METHODS

Four locations were selected for this study, three eco-restored sites named as Aranya, Merveille, Sakthi and Puthupet, is sacred grove (Figure 1). These four sites are under the jurisdiction of Villupuram district, Tamil Nadu State. Geologically, the soil is red ferrallitic and belonged to the formation of 'Cuddalore sandstone intrinsic type' during Miocene period (Meher-Homji, 1970). This study area falls in typical maritime tropical climate with dissymmetric rainfall regime. The mean annual rainfall was 1256 mm within 56 rainy days per year was recorded between 2007 and 2018 (Balachandran, 2016). The minimum temperature 17.7 °C was recorded in January and the maximum 40.5 °C in May and the mean is 28.5 °C. The average relative humidity is 76% and the weather is generally cool during December to January with the late nights dewy. Dry weather prevails during April to June. Wind speed ranges from 5-9 km/h during July to September and higher during the cyclonic days, during October to December (Meher-Homji, 1974).

Figure 1 Four study areas for the parasite: *Dendrophthoe falcate*

Regular field survey three days in a week was conducted between the months of October 2017 and March 2018, enumerated *D. falcata* (DF) infected plants in all the sites. To know the similarity and differences between the host and parasite's leaf, stem, haustorium and epicortical root was taken into account for this study. The similarity and differences was observed in morphological and floral parts of plants; then collected, measured and weighed the leaf area and biomass; and photographed the versatile characteristic features. In addition haustorium samples was also collected to study the bark features (colour, nature of lenticels, smooth / roughness, peeling); growth and establishment of epicotrical root over the host; and noticed colour difference at cross cut of DF stem between host and parasite. By following Calvin and Wilson, (1998, 2006) and Shanavas Khan and Sivadasan, (2009) methods was followed to categorise the haustorium into three kinds of morphotypes depends on their growth and establishment. This study established three morphotypes into three types of defence mechanism based on their susceptibility or resistance nature occurred between them and they were described for further understanding.

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3. RESULTS

The DF infected host species was enumerated during the course of study and a total of 64 species was recorded from all four sites. Among them Aranya forest and sanctuary recorded with maximum number (34) of hosts followed by Shakti (27), Merveille (26), and minimum (5) was recorded at Puthupet. This study has recorded 27 out of 64 species first time as new host to DF (Table 1) from India. The 64 species were represented from 51 genera and 25 families, of which 42 are native and 22 exotics. Maximum number of DF infection was found in the family Leguminosae (18 species) followed by Rutaceae and Sapotaceae had 5 species each and 4 from Rubiaceae. Most affected genus is *Acacia* (5 species) and 3 species each was noticed on *Albizia* and *Dalbergia*. This study also found Combretaceae, Cordiaceae, Loganiaceae and Sapindaceae are the new host family record.

Table 1 Enumeration of DF infected species from the four sites

No.	Host name	Family Name	Aranya	Shakthi	Merve	Puthupet	Ex/Nat
1	Acacia auriculiformis	Leguminosae	1	1	1	0	Exotic
2	Acacia chundra	Rutaceae	1	0	0	0	Native
3	Acacia colei *	Leguminosae	1	0	1	0	Exotic
4	Acacia holosericea	Leguminosae	1	0	1	0	Exotic
5	Acacia mellifera *	Leguminosae	1	0	0	0	Exotic
6	Achrus sapota	Sapotaceae	0	1	0	0	Exotic
7	Aegle marmelos	Rutaceae	0	1	0	1	Native
8	Albizia guachapele *	Leguminosae	0	1	0	0	Exotic
9	Albizia lebbeck	Leguminosae	1	1	1	0	Native
10	Albizia richardiana *	Leguminosae	0	0	1	0	Exotic
11	Annona squamosa	Annonaceae	0	1	1	0	Exotic
12	Bauhenia racemosa	Leguminosae	1	0	0	0	Native
13	Careya arborea	Lecythidaceae	0	0	1	0	Native
14	Casuarina equisetifolia	Casuarinaceae	1	1	1	0	Native
15	Casearia ovata *	Salicaceae	1	0	0	0	Native
16	Ceiba pentandra	Malvaceae	0	0	1	0	Exotic
17	Chloroxylon swietenia *	Rutaceae	1	1	0	0	Native
18	Cordia subcordata *	Boraginiaceae	0	1	0	0	Exotic
19	Couropita guanensis *	Lecythidaceae	0	1	0	0	Exotic
20	Dalbergia lanceolaria	Leguminosae	1	0	1	0	Native
21	Dalbergia latifolia	Leguminosae	1	0	0	0	Native
22	Dalbergia sissoo	Leguminosae	0	0	1	0	Native
23	Dolichandrone falcata *	Bignonaceaea	1	0	0	0	Native
24	Ehretia pubescens	Boraginiaceae	0	1	0	0	Native
25	Ficus benghalensis	Moraceae	1	1	1	0	Native
26	Ficus religiosa	Moraceae	1	0	0	0	Native
27	Gmelina arborea	Lamiaceae	1	0	1	0	Native
28	Grevillea robusta	Proteaceae	0	0	1	0	Exotic
29	Guettarda speciosa *	Rubiaceae	0	1	0	0	Native
30	Hardwickia binata	Leguminosae	1	0	0	0	Native
31	Helicteres isora *	Malvaceae	1	0	0	0	Native
32	Hibiscus rosa-sinensis	Malvaceae	0	1	0	0	Exotic
33	Holoptelea integrifolia	Ulmaceae	1	0	0	0	Native
34	Ixora pavetta *	Rubiaceae	1	1	0	0	Native
35	Labromia bojeri *	Sapotaceae	0	1	0	0	Exotic

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36	Lannea coromandelica	Anacardiaceae	1	0	1	0	Native
37	Lepisanthes tetraphylla *	Sapindaceae	0	0	0	1	Native
38	Magnifera indica	Anacardiaceae	1	0	0	0	Native
39	Manilkara hexendra *	Sapotaceae	0	0	1	0	Native

Two growth pattern *viz*. erect (upward branching) and pendulous (downward branching) kinds were observed for the first time in DF from this study. Well established pendulous growth pattern up to 2.5 m was noticed on the host species such as *Albizia lebbeck, A. saman, A. quachepalae, Casuarina equisetifolia, Lepisanthes tetraphylla, Morinda coreia, Pongamia pinnata* and few others. In erect type, stunted growth pattern was noticed on *Cordia subcordata, Dolichandrone falcata, Gmelina arborea, Hardwickia binata, Memecylon umbellatum, Strychnons nux-vomica* and others (Figure 2).

Albizia lebbeck is the only one native species common in all four sites and *Acacia auriculiformis* is the exotic species occurred in three man made vegetations got infected heavily by DF. Most individuals of *A. lebbeck* and *Morinda coreia* was infected in all three manmade forests. The infection of DF more than one branches of the same tree was found at *A. lebbeck*, *Casuarina equisetifolia*, *Gmelina arborea* and *Pongamia pinnata*, of which *A. lebbeck* was highly susceptible and leads to casualty (Figure 2).

Erect on *Dolichandrone falcate*

Erect &pendulous on *Albizia guachepalae*

Figure 2 Growth pattern of DF. **2a** Two different growth pattern of DF

DF on *Acacia auriculiformis*

DF on *Albizia lebbeck*

2b Establishment and death of DF

Morphological relationship

Leaf (area and thickness), stem (bark, lenticels and branchlets cut end), and haustorium (3 morphotypes) morphology between the host and DF was studied.

Leaf Morphology

Twenty species from 19 genera and 13 families, including simple and compound leaves were selected. Leaf thickness measured in all 20 species where as leaf area and biomass was studied only in 14 simple leafed species.

Leaf area of 14 host and their respective DF leaves was compared, in which 9 pairs have positive correlation where as one species (*Manilkara hexandra*) has negative result and 4 species *viz*. *Cordia subcordata*, *Gmelina arborea*, *Labromia bojeri* and *Mangifera indica* have wide difference (Figure 4). However, significant correlation in leaf shape, base, and apex between both taxa was observed in most species (Figure 3). The leaf area of DF generally ranging from 31.49cm^2 (*Hardwickia binata*) to 61.51cm^2 (*Acacia*

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colei), however extraordinary leaf area 255.72cm^2 was recorded on *Pongamia pinnata*. Significant relationship, 16 out of 20 pairs was found in leaf thickness study whereas the remaining four species *viz. Albizia lebbeck*, *Cordia subcordata*, *Gmelina arborea* and *Hardwickia binata* were characteristically thinner (Figure 4).

Mangifera indica and DF

Strychnos nux-vomica and DF

Figure 3 Leaf Area: Morphological similarity of the host leaves with DF leaves. **3a** Similar size and shape of host and DF leaves.

Albizia lebbeck

Gmelina arborea

3b Similarity and differences in lenticels

Mangifera indica

Guetarda speciosa

3c ER and host new leaf

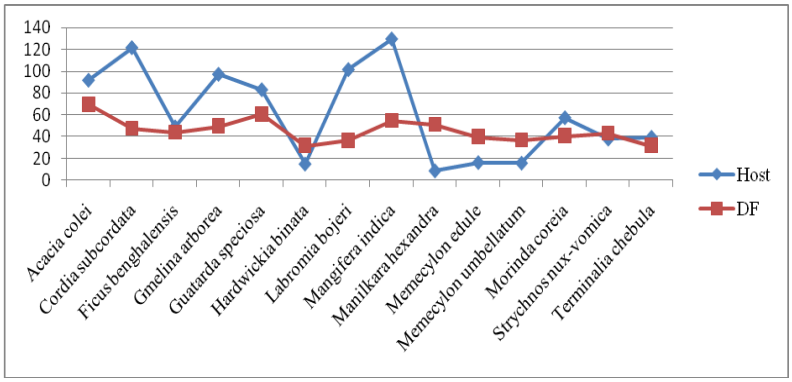
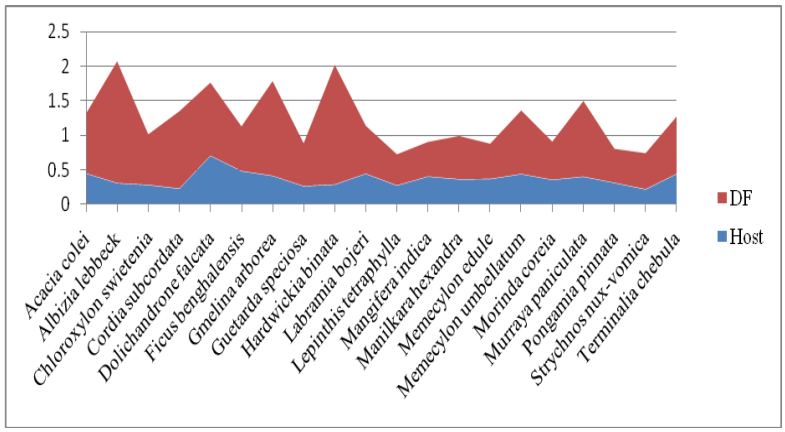


Figure 4 Morphological relationship of the host and DF leaves

4a Leaf Area.



4b Leaf Thickness

Stem Morphology

The stem bark, lenticels and cut end of branchlets among the taxa were studied. Distinct differences was observed from the bark colour, lenticels and surface features on DFs stem where growing on the host such as *Acacia chundra*, *Gmelina arborea*, *Hardwickia binata*, *Helicteres isora*, *Lepisanthes tetraphylla*, *Manilkara zapota*, *Strychnos nux-vomica* and *Tectona grandis* (Figure 5). The presence or absence, size, shape and orientation of lenticels on the epicortical roots are very clearly representing the characters of their host stem in *Albizia lebbeck*, *Dolichandrone falcata*, *Gmelina arborea*, *Helicteres isora* (Figure 3). Additionally, the cross cut end of DF stem colour when compared with cross cut portion of stems from *Acacia colei*, *Casuarina equisetifolia*, *Ceiba pentandra*, *Dolichandrone falcata*, *Hardwickia binata*, *Helicteres isora* and *Strychnos nux-vomica* was significantly varied (Figure 5).

Gmelina arborea

Manilkara zapota

Helicteres isora

Strychnos nux-vomica

Figure 5 Stem morphology of host and DF – similarities and differences. **5a** Similarities in bark between DF and host

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DF stem from *Dolichandrone falcata* DF stem from *Hardwickia binata*

5b Differences in stem cut ends of DF

Haustorium Morphology

The colour of epicortical root (ER) meristem and the new flush of host are matching each other in most species. For example, *Albizia lebbeck*, *Guetarda speciosa*, *Pongamia pinnata* and *Tabernamontana coronaria* and others apical meristem of ER and their host new leaves are green whereas pink colour was found from *Mangifera indica* and *Memecylon umbellatum* (Figure 3).

A total of 25 haustoria out of 64 species were collected and studied the morphology of haustorium based on their growth and establishment, the interaction with the host by parasite and the ER with or without branches. About 8 species haustoria represented clasping union (CU), 11 for wood roses (WR) and 11 for epicortical roots (ER) categories (Table 2). In addition, this study also found 1) Single ER with 2-4 noded haustoria, 2) branched ER with many haustorial nodes and 3) even and uneven shapes of wood roses (Figure 6).

Table 2 DF Haustorium and its morphotypes recognised from this study (Calvin and Wilson 1998).

Sl. No	Species Name	Clasping union	Wood Roses	ER
1	Acacia auriculiformis	0	1	1
2	Albizia lebbeck	0	1	1
3	Annona squamosa	0	0	1
4	Casearia ovata	0	0	1
5	Ceiba pentandra	0	1	0
6	Cordia subcordata	1	0	0
7	Dalbergia lanceolaria	0	1	0
8	Dolichandrone falcata	1	1	0
9	Gmelina arborea	1	0	0
10	Guetarda speciosa	0	1	0
11	Hardwickia binata	0	0	1
12	Helicteres isora	1	0	1
13	Labramia bojeri	0	1	0
14	Lepisanthes tetraphylla	1	0	0
15	Magnifera indica	0	0	1
16	Manilkara hexandra	0	1	0
17	Manilkara sapota	1	0	0
18	Memecylon edule	0	0	1
19	Memecylon umbellatum	0	1	0
20	Morinda corea	1	0	1
21	Murraya paniculata	0	0	1
22	Pongamia pinata	0	0	1
23	Pterocarpus santalinus	0	1	0
24	Strychnons nux-vomica	0	1	0

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25	Syzygium cumini	1	0	0
	Total	8	11	11

Defense mechanism

The analysis from 25 samples three kinds of defense mechanism was proposed from three morphotypes (CU, ER and WR). The morphotype clasping union (CU) was treated as host dominants; wood roses (WR) considered as parasite dominants and epicortical root (ER) observed as equipotent. This study found 27% (8) of species as host dominant, 36% (11) are parasite dominant and 37% (11) belonged to equipotent category (Table 2).

Host dominants

Means host dominated haustorium, in which the host's stem growing faster and enveloping the parasitic haustorial base. Owing to the clamp formation by the host was completely regulated the growth and development of the parasite. By formation this haustorium is inseparable even after death of the parasite. Generally the parasite develops only one primary haustorium and rarely develops up to 3 secondary haustoria, connected by ER. In this type the parasite grows erect, up to maximum of one m high, with thick (sometimes thin) branchlets, leaves small in size, much thicker than usual are the easy identifiable features of host dominant haustorium. There are 8 out of 25 species: *Acacia coleia*, *Cordia subcordata*, *Dolichandrone falcata*, *Gmelina arborea, Manilkara zapota*, *Morinda coreia* and *Syzygium cumini* are the best examples observed to this category (Figure 6).

Gmelina arborea (single & like clamp) *Dolichandrone falcata* (multi & foliaceous)

Figure 6 Three major morphotypes of haustorium. **6a** Host dominant – Clasping union category

Acacia auriculiformis *Albizia lebbeck*

6b Parasite dominant – Wood roses category

Ceiba pentandra - UH with aerial ER *Pongamia pinnata* - MH with many ER

6c Equipotent - Epicortical root category

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Parasite dominants

Means parasite dominated haustorium, in this category the host susceptible against the parasite. In which the haustorium could be separated into two portions after the death of host or parasite, and they are called as wood rose or flower. Examples are *Acacia auriculiformis*, *Albizia lebbeck*, *Ceiba pentandra*, *Chloroxylon swietenia Dlabergia lanceolaria*, *Guetarda speciosa*, *Labramia bojeri*, *Manilkara hexandra*, *Memecylon umbellatum*, *Pterocarpus santalinus* and *Strychnos nux-vomica* (Figure 6). The easy identifiable features are: well established growth of the parasite, both erect and pendulous nature of growth up to 2.5 m long, bigger in size of haustorium up to 20 cm wide, thick branches and branchlets, lush growth of leaves, and leaf area sometimes reached 60 cm^2 are the main characters of this category. Interestingly this study was found a DF growing more than 10 years on *Albizia saman* tree along the avenue in the city of Puducherry. There are 11 species belonged to this category out of 25 samples studied.

Equipotent haustorium

In this type the host and parasite are equally defending each other. The parasite develops branched or unbranched ER up to 2 m long or/and the occurrence of many secondary nodes or haustoria at regular intervels. This group was further subdivided into two types: 1. Unihaustorium (UH), rarely two with hanging (aerial) ER and 2. Multihaustorial (MH) nodes with long creeping ER. The unihaustorium category has simple or branched aerial ER and it was found in *Annona squamosa*, *Ceiba pentandra*, *Strychnos nux-vomica* and *Terminalia chebula* (Figure 6). The second type was found in *Ficus benghalensis*, *Hardwickia binata*, *Mangifera indica Memecylon edule* and *Pongamia pinnata* (Figure 6). Presence of aerial ERs or multihaustorial nodes, multi branching pattern of stem growth with thin branchelets is the main characters of this kind. Long epicortical roots all along the host stem were recorded in *Albizia lebbeck*, *Ficus benghalensis*, *Memecylon edule* and *Pongamia pinnata*. About 11 species were belonged to this type.

4. DISCUSSION

Since Fischer, (1907) to Rothe and Maheshwari, (2017) adding host range records to DF and they are endless. Recently Suavaathimani, (2018) and Vinothini, (2018) were also recorded four new family additions and new host records (27/64) that studied from four sites at Villupuram districts of Tamil Nadu, southern India. This study was more optimistic with the statement of Downey, (1998) *i.e.* 'several mistletoe species opportunistically parasitised exotic species as well as native species, the significance of which is poorly understood'. But Kuijt, (1979) and Kuijt and Hansen, (2015) expressed that the host preferences or host ranges are difficult to establish in terrestrial parasitic members of the order Santalales for practical reasons. And the remarks of Pennings and Callaway, (2002) study, the parasite has profound effects on different plant communities in which they occur but they are often and still ignored in community theory was highly considerable.

Grevillea robusta and *Punica granatum* was reported as common host by Vijayan *et al*., (2015); *Chloroxylon switenia, Boswellia serrata, Madhuca longifolia,* and *Anogeissus latifolia* by Rothe and Maheswari, (2017); *Cassia siamea*, *Acacia auriculiformis* and *Samanea saman* by Selvi and Kadamban, (2009). This study was recorded *Albizia lebbeck* as the only native species in all four sites and *Acacia auriculiformis* at three man made vegetation have heavily infected and leads to casualty by DF. This result strongly proves the statement of Aukema, (2003) that "in most extreme cases, heavy mistletoe infestation may result in host death". In addition, "a common host in one area may turn out to be merely a secondary one in a different locality" is also likely considered (Kuijt and Hansen, 2015).

Morphology

Generally, DF shows polymorphic features in leaves (size and shape), flowers (colour variation), stamen (presence or absence of pubescence on the stalk), fruit (colour, size and shape) and in haustorium (three morphotypes) (Barlow, 1995). This study recorded polymorphic growth pattern erect and pendulous nature from DF for the first time. The results of leaf area and thickness between DF and their host species was positive and appropriate very much with the study of Barlow and Wiens, (1977), Pannell and Farmer, (2016) *i.e*. the parasitic plants mimic their host's foliage size and shape and enjoy benefits of protection from potential predators (Batesian mimicry) was recognized. Whereas Ehleringer *et al*., (1986) and Bannister, (1989) was placed an open debate about the relationship between mistletoe foliar quality and mimicking for the herbivores.

Characteristically, the family Loranthaceae have thick and brittle leaves whereas the size and shapes are highly variable. Even though the results from this study such as leaf area (9/14) and leaf thickness (16/20) of host and DF pairs have strong positive correlation. This distinct similarity between them was strongly supporting the Batesian mimicry concept; that is the changes in size and shape of leaves might be developed due to adaptations or mutual beneficiary.

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In addition to leaf characters, interestingly this work was also observed the similarities in stem characters *viz*. stem cross cut end (colour), and bark (colour, lenticels, surface). Positive results were also found at apical meristem of ER and new flush colour of the host. These results are complementary and strongly representing that there might be a strong relationship between them and also satisfactorily accepting the concluding remark of Downey, (1998). In addition with the strong morphological relation with leaf and stem characters from this study once again prove the statement of Pannell and Farmer (2016), *i.e*. the parasite generally mimicking the characters of the host plant. Preliminary report of Vinothini *et al*., (2018) was an additional support to this study.

Defence mechanism

The study based on the haustorial morphotypes (Calvin and Wilson, 1998, 2006; Devkota and Glatzel, 2007), and the two haustorial portions (Shanavaskhan and Sivadasan, 2009; Kuijt and Hansen, 2015) this work was categorized three kinds of defence mechanism *viz*. the morphotype CU was considered as Host Dominant (HD), WR treated as Parasite Dominant, and ER related to Equipotent (EP). The proposition of defence mechanism was influenced by the study of Kuijt and Hansen, (2015) and Kuijt and Lye, (2005). The formation of wood roses due to xylem-xylem continuity has logical and the study of Devkota and Glatzel, (2007) was also to be significantly considered. In addition Devkota and Glatzel, (2007) concluded that the wood roses or the clasping union are considered to be intermediate in evolution among the aerial Loranthaceae and the epicortical root bearing genera or root borne shoots are considered to be ancestral as compared to those without them. For which further precise anatomical studies will pave the way to understand these relations.

In Asian Santalaceae, especially in some *Dendrophthoë* species Kuijt, (1990) found that the haustoria bearing epicortical roots and the tips being lodged in bark crevices of the host but the conclusive evidence for this is not available. Remarkable observations were recorded from this study, such as branched and unbranched ER with single or multi-haustorial nodes; aerial ERs; ER running parallel towards the main and side branches of the host up to 2 m long (creeping ER); new ER hyperparasitize on old ER; growing on the smooth, corky and fissured barks. These results were recognized that the parasite develops strong interaction with the host in different mode to get water and nutrition but the host regulated the penetration and further establishment of the parasite. This study was favoured by Kuijt's, (1969) concluding remark that the host species may play a role in determining the parasitic constituents, host resistance to haustorial penetration and chemical incompatibility. In all, this work strongly concluded that the leaf (size, shape, thickness, leaf area) and stem traits (bark, lenticels) of the parasite have morphologically mimicking the host whereas the growth and establishment of the parasite are due to mutual influence or defence mechanism between them. Near future, the anatomical, phytochemical, physiological, molecular, metabolic and genetic studies may support to know the exact coherence between the two taxa.

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Author contributions

The first author conceived the study, identified the study area and host species, framed the methodology, analysed the data and concluded; all authors conducted the field survey and collected voucher samples; SS and VK drafted the manuscript; and all authors approved final version for the publication.

Ethical approval

Dendrophthoe falcata infected plants & plant materials were used in the study. Samples were collected for Villupuram district, Tamil Nadu, India. The ethical guidelines for plants & plant materials were followed in the study for sample collection, identification & preservation.

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Conflicts of interests

The authors declare that there are no conflicts of interest.

Data and materials availability

All data associated with this study are present in the paper.

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